

INTRACRANIAL MOVEMENT IN THE COELACANTH *LATIMERIA CHALUMNAE* SMITH (OSTEICHTHYES, CROSSOPTERYGII)

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ABSTRACT

The intracranial kinesis of the coelacanth fish *Latimeria chalumnae* Smith was studied from motion picture records of manipulation of the skull of a "fresh" dead specimen. Frame-by-frame analysis provided data on the relationships between change in angle of the gape and the angle at the intracranial joint. The length relationships of the subcephalic and geniocoracoid muscles during the mouth-opening sequence were noted. The data suggest that anterior movement of the shoulder girdle is an important feature of the intracranial mechanism and that such movement allows the geniocoracoid to contract essentially isometrically when the gape is opened. The possible function of cranial kinesis is discussed.

INTRODUCTION

For many years one of the most interesting aspects of the morphology of the Coelacanthini, and their close relatives the wholly fossil Rhipidistia, has been the special mechanism of intracranial kinesis, a major feature of which is the division of the braincase into halves with the "intracranial joint" between them. The anterior functional unit of the skull (anterior braincase, cheek, palate and lower jaws) is movably attached to the posterior unit (posterior braincase, gill apparatus and trunk). The structure and probable mode of action of the skull in these fishes have been discussed by several workers (see Thomson, 1967, 1969 for reviews of these subjects), but no worker has yet been able to study this system in live specimens of *Latimeria chalumnae* Smith, the only extant crossopterygian. While the possible adaptive role of intracranial kinesis in crossopterygians (and indeed other vertebrates) has often been debated, the situation is still far from clear. Presumably the special advantages of such a system must lie in part in the mode of opening and closing the gape, the special orientation of the gape, the extent of gape opening and the mode and force of gape closure.

According to most authorities (see review by Thomson, 1967), the principal muscle involved in the crucial dorsal flexure of the intracranial joint of crossopterygians is the paired *M. geniocoracoideus* lying on either side of the ventral midline. This is also the principal mandibular retractor (Millot and Anthony, 1958). It has been supposed that by virtue of the mechanical arrangement of the various skull parts, the action of this muscle in retracting the mandibles and rotating them ventrally around the quadrate joint includes translation of the ventrally and posteriorly directed forces into a force pushing the palate and anterior portion of the braincase forward and upward. During this process (Fig. 1), again by virtue of the shape and arrangement of the palate, the mandibles are actually projected considerably forward. At first sight, therefore, it would seem that the length of the *geniocoracoideus* muscles would in fact increase during this process (Fig. 1) rather than remain constant or decrease as one would expect if their contraction is the prime mover in this process. Closure of the gape is a more complicated process. There is a special paired subcephalic muscle (see Millot and Anthony, 1958) that lies along the ventral surface of the endocranium and is responsible for "adduction" of the anterior unit of the braincase (ventral

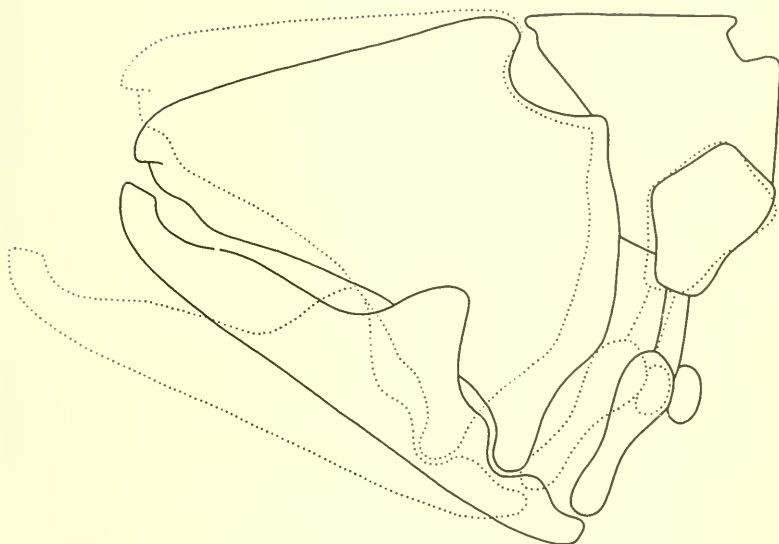


FIG. 1. *Latimeria chalumnae*. Outline drawings of the braincase, palate, hyoid arch and lower jaw showing the relative positions of the skull components when the gape is closed (solid lines) and when the gape is opened and the intracranial joint flexed dorsally (dotted lines). Redrawn from Thomson, 1969.

rotation at the intracranial joint). The gape itself is closed by the large mandibular adductors, both the origins and insertions of which lie wholly within the anterior skull unit. The anterior skull unit may also be retracted by the musculature associated with the ventral hyoid skeleton. This paper examines the length relationships of the genioacoracoideus and subcephalic muscles (see Fig. 2) during intracranial kinesis in *Latimeria chalumnae* with the hope of further elucidating their roles in this complex process.

In the absence of live material and in the face of many logistic difficulties before live material of this large rare fish can be worked within a laboratory situation, we based the present study on observations made upon a specimen preserved fresh by freezing immediately after capture. The specimen [YPM 1482 (Yale Peabody Museum); see

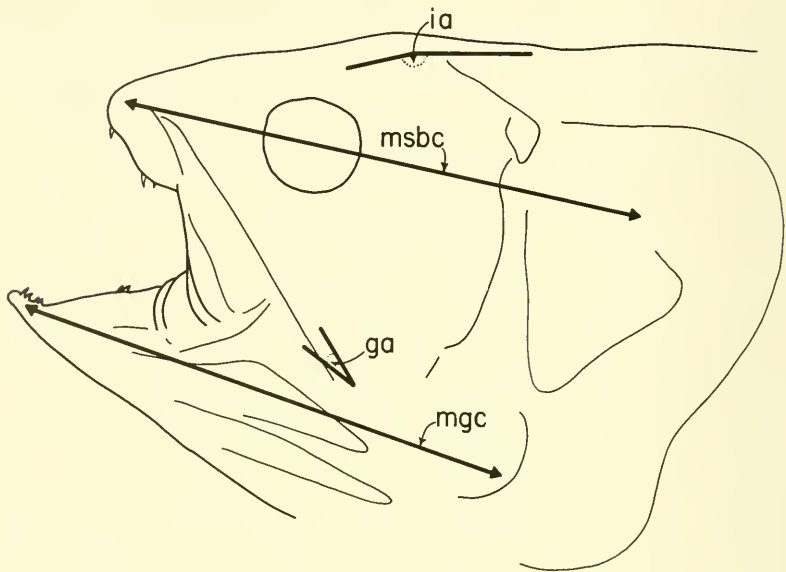


FIG. 2. *Latimeria chalumnae*. Outline drawing made from motion picture record of dead specimen showing dimensions and angles measured. Specimen YPM 1482, Fish Collection, Yale Peabody Museum of Natural History; total length 107 cm, fresh weight 15.87 kg, (ga = angle of gape; ia = angle at intracranial joint; mgc = estimate of length of *M. geniocracoideus*; msbc = estimate of length of *M. subcephalicus*).

Thomson, 1966a, b] was thawed in the laboratory and the skull carefully manipulated to observe the sequence of movements involved in opening the gape. It was not felt that the process of gape closure could be simulated with any degree of accuracy because there is no way of predicting the sequence of operation of the separate subcephalic and adductor mandibulae systems (see below). The sequence of movements during opening of the gape and accompanying dorsal flexure at the intracranial joint was recorded in motion pictures for subsequent frame-by-frame analysis, a series of markers having been attached to the head of the fish. From drawings made from the film while projected (Fig. 2), measurements were made of the distances between origin and insertion of the geniocracoideus and subcephalic muscle systems. These measurements are used in the following analysis as an estimate of the lengths of these muscles during opening of the gape. The dimensions of the specimen are indicated in Figure 2.

RELATIONSHIP BETWEEN THE ANGLE OF THE INTRACRANIAL JOINT AND THE ANGLE OF THE GAPE

From the film record it was seen that opening of the gape (depression of the mandibles) was accompanied by simultaneous dorsal rotation (extension) at the intracranial joint. The relationship between the two angles is shown in Figure 3, and it will be noted that the curve

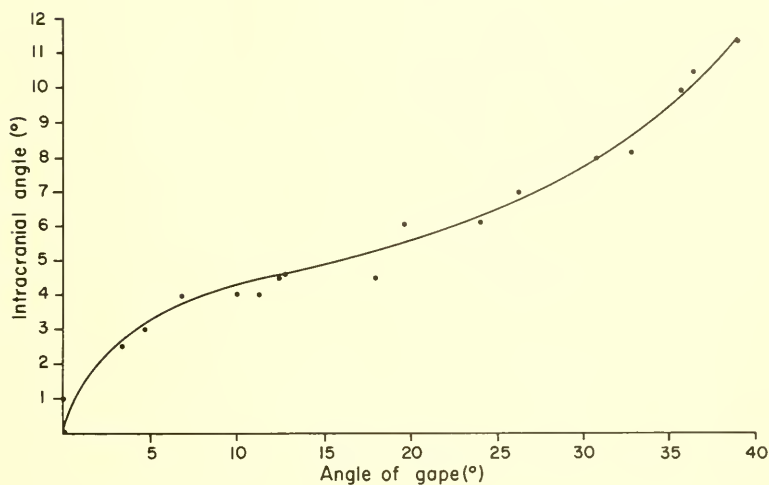


FIG. 3. *Latimeria chalumnae*. Graph showing probable relationship between angle of gape and angle of intracranial joint during the sequence of opening the mouth.

has a sigmoid shape. Certain points have to be noted, here, however. In manipulation of the skull it was seen that in the "inert" position, with the gape closed, the intracranial joint was bent slightly downward. Apparently, in life this did not occur and the slight sagging of the anterior portion of the skull in our specimen was probably due to a general lack of muscle tonus and notochordal elasticity. If so, it may well be that in life the initial phases of mandibular depression (perhaps 0° to 5°) occurred without change in the angle of the

intracranial joint. It is also possible that, during the sequence of manipulation, in attempting to simulate the forward thrusting of the mandibles this action was overemphasized. The final part of the graph (Fig. 3) is therefore slightly suspect (gape opening between 35° and 40°).

LENGTH RELATIONSHIPS OF *M. GENIOTORACOIDEUS*

From motion picture analysis, the length relationships of *M. genio-
coracoideus* are somewhat puzzling. As Figure 4A shows, when the angle of the gape increases, the distance between the origin and insertion of the genio-
coracoideus increases in a regular manner. Figure 4B shows, however, that the initial phases of dorsal intracranial extension are not correlated with a change in length of this muscle until the

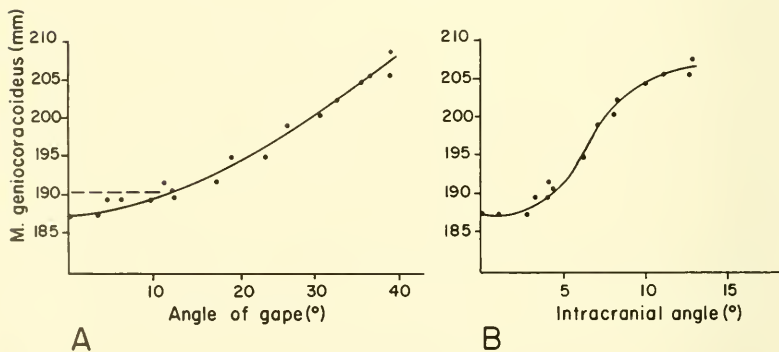


FIG. 4. *Latimeria chalumnae*. Graph showing probable relationship between change in length of *M. genio-
coracoideus* and (A) angle of gape and (B) angle at intracranial joint during sequence of mouth opening ("resting length" 187 mm).

intracranial joint has been moved through about 3° (20% of total flexure). The graph of the total relationship is a sigmoid curve. During opening of the mouth, *M. geniocoracoideus* increases in length by about 12%. This therefore seems to document the paradox that the muscle that is assumed to be the main mandibular retractor and the prime mover in dorsal rotation at the intracranial joint may actually increase in length in the process of opening the mouth. It is indeed difficult to visualize how a muscle with this type of relationship could activate this system. There are several possibilities for resolution of this dilemma: 1) It is possible that the point of insertion of the muscle onto the shoulder girdle is moved forward during the sequence (by action of the axial musculature), thus allowing net shortening of the muscle. 2) It is possible that, as noted previously, the anterior skull unit is normally held at a slightly extended (dorsal) angle during the initial part of gape opening. If this were the case, then at this time retraction of the mandibles would not have been accompanied by movement at the intracranial joint. In Figure 5, a reconstruction

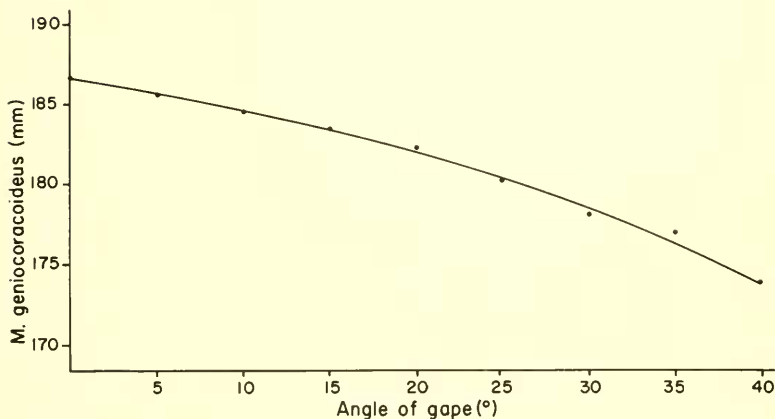


FIG. 5. *Latimeria chalumnae*. Estimated relationship between change in length of *M. geniocoracoideus* and angle of gape when there is no movement at the intracranial joint (from graphical reconstructions).

is given of the relationship between geniocracoid length and gape angle in a sequence of mandibular retraction without intracranial movement (made from a graphical reconstruction, this is presumably impossible in life). In this case, the muscle shows a steady decrease in length (approximately 7%). Given the imperfection of our techniques, it seems reasonable to suggest that during the early phases of opening the mouth, *M. geniocracoideus* was contracting isometrically (Fig. 4A, dotted line). This does not, however, resolve the paradox of increase in length of this muscle during the later stages of mouth opening. 3) A third factor that may be involved is the contraction of other muscles, such as the *MM. sternohyoideus*. This has been discounted as a factor in mandibular retraction by Millot and Anthony (1958) and Thomson (1967) but it is worth raising the possibility that some other muscle system is involved in the later phases of gape opening. Having mentioned these three possibilities, I should observe that the first of these seems to me the most plausible.

In my 1967 study of crossopterygian intracranial kinesis, I suggested that flexure of the intracranial joint might be possible without opening of the gape in coelacanth (but not Rhipidistia). This might be associated with respiratory movements of the head (see also Thomson, 1969). Figure 6 shows the length relationships of *M. geniocracoideus* under such conditions (from a graphical reconstruction). It will be seen again that the length relationships strongly indicate that anterior movement of the shoulder girdle would be necessary in order for *M. geniocracoideus* to maintain a constant length or to contract during this sequence. Indeed, I suggest that these data provide firm evidence supporting the postulation of such a movement. The data also indicate that a minimum forward movement of the coracoid through 12% of the resting length of the muscle (21 mm in this fish) would be necessary to achieve isometric contraction of the *M. geniocracoideus* in normal opening of the gape.

LENGTH RELATIONSHIPS OF THE SUBCEPHALIC MUSCLE

The probable relationships of this muscle were estimated from the change in length of the straight-line distance between the origin and insertion of this muscle during mouth opening. In fact, this muscle has a considerable tendinous insertion at the front of the palate. As shown in Figure 7, the relationships between the overall length and

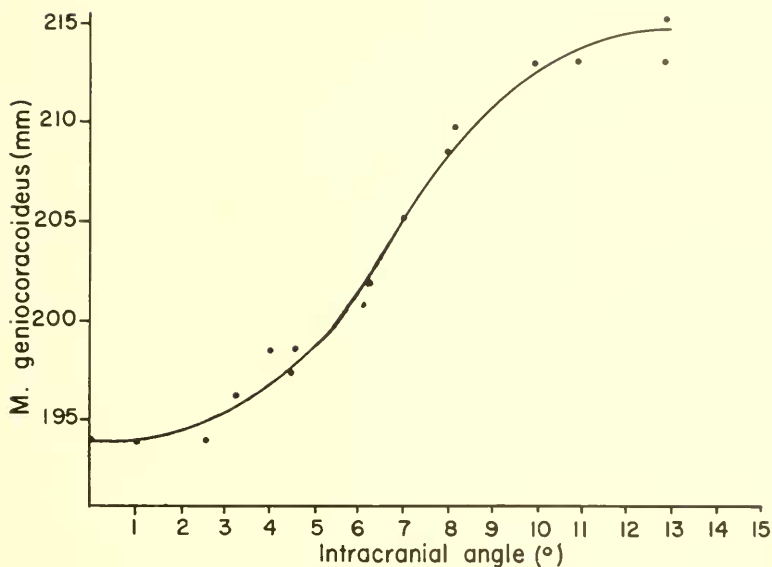


FIG. 6. *Latimeria chalumnae*. Estimated relationship between change in length of *M. geniocoracoideus* and angle at intracranial joint when there is no depression of the mandibles (from graphical reconstructions).

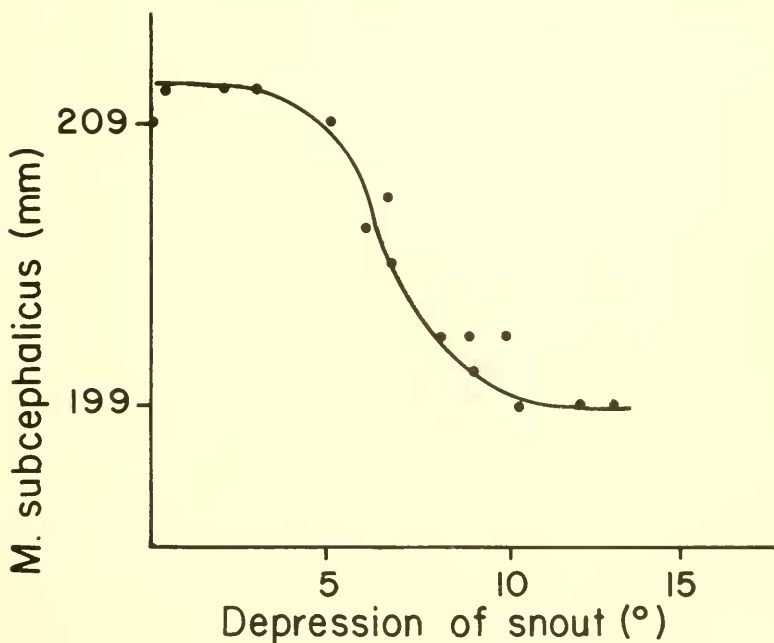


FIG. 7. *Latimeria chalumnae*. Graph showing probable relationship between change in length of *M. subcephalicus* and angle at intracranial joint, during depression of the snout ("resting length" 200 mm).

the angle of the intracranial joint are complicated. Due to the configuration of the skull, the changes in length describe a sigmoid curve. However, it must be noted that the total change in length of the muscle-tendon combination is in fact only some 5.5% of the resting length which presumably indicates that contraction is virtually isometric when the snout is being depressed. Since the sequence of separate activation of the subcephalic muscles in depressing the snout and the mandibular adductors cannot be determined from dead material, the relationship between change in the intracranial angle and the angle of the gape in closing the mouth cannot be measured.

DISCUSSION

A surprisingly large number of vertebrates, from the Paleozoic arthrodiros (see, for example Miles, 1969) to the lizards and snakes, possesses a system whereby the skull or some part of it can be elevated as the mandibles are depressed. In the Actinopterygii perhaps an analagous system is the protrusion of the upper jaws, which may also be accompanied by a raising of the head (see Schaeffer and Rosen, 1961; Alexander, 1968). In many of these animals, structures of the trunk play an important role in dorsal extension of the head. This movement may involve axial muscles, inserted on the occipital region, or the shoulder girdle to which muscles of the branchial apparatus and jaws are attached. In the Crossopterygii, living and fossil, intracranial kinesis, operating around a joint in the mid-part of the braincase, is a unique system and of considerable interest. Because we know so little about the biology of crossopterygians, even the living species *Latimeria chalumnae*, one is hesitant to try to draw general conclusions from so imperfect a set of data and methods as those presented here. Nonetheless, there seems to be some support here for the intuitively acceptable conclusion that the operation of intracranial kinesis during opening of the gape must be accompanied by a forward rotation of the ventral coracoid region of the shoulder girdle by the muscles of the trunk. If this is not the case, then an extremely puzzling situation exists with respect to the mode of action of the geniocoracoideus muscles that seem to be the prime agents in opening the gape and elevating the snout.

Unfortunately this study has not shed light on the mode of action

of the subcephalic muscles and the adaptive role of depression of the anterior skull unit in closure of the mouth. If the subcephalic muscles are brought into play during the early phases of gape closure, their role might be to provide an immediate rapid downward and backward movement of the palatal dental battery, ensnaring the prey from above while the mandibles are as yet in an early stage of adduction. This would have the interesting effect of reducing the absolute upward movement of the mandibles at this point. However, it would have no effect on the movement of the mandibles relative either to the palate or to the prey since all three are functionally part of the same anterior skull unit during this time. Similarly, this would not reduce the force of mandibular adduction. The combined movement of the anterior skull unit is also rearward during this process, having the effect of bringing the prey further into the gullet. The alternative hypothesis, i.e., that contraction of the subcephalics does not occur until later in the sequence of gape closure, is also acceptable in terms of the estimates made here of the length relationships of the subcephalic muscles. However it is difficult to see what advantage such a system might have, except possibly with respect to forcing the prey down into the gullet once it had been assaulted by the mandibles. The intracranial kinesis may also be used alone in respiratory movements but in this case it is necessary to find some kind of compensatory action, probably movement of the shoulder girdle, to allow appropriate contraction of the geniocoracoides muscles.

One of the interesting features to the author of making such a study as this is that it is in some sense predictive. One can only hope that before too long such a study may be followed by direct observation of the feeding mechanism of a live coelacanth.

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